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# The trophic status of the fish fauna in Lago Camaleão, a macrophyte dominated floodplain lake in the middle Amazon

by

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**Abstract**

Food offer and consumption by the fish fauna were studied at medium and high waterlevels in a macrophyte dominated and strongly hypoxic floodplain lake of the middle Amazon. Detritus was shown to be the main food item, followed by terrestrial invertebrates and periphyton. Low aquatic macrophyte consumption is related to its low nutrient value in comparison with other abundant foods and its seasonal availability.

Keywords: **Fish, feeding, Amazon, floodplain, ecology.**

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## 1. Introduction

Because of their species diversity, heterogeneity, abundance and mobility fish have a key function in food webs of aquatic ecosystems. Specialists and generalists are able to use a very wide spectrum of food items. In tropical floodplains, for instance the floodplain of the Amazon and its big tributaries, this capacity is particularly well documented because of the great diversity of the fish fauna and the enormous variety of food offered as a result of the inundation cycle.

Several authors have already studied the food and feeding habits of some Amazonian fish species (MARLIER 1968; LOWE-McCONNELL 1969; KNÖPPEL 1970; HONDA 1974; SAUL 1975; CARVALHO 1979; SOARES 1979; ALMEIDA 1980; PAIXÃO 1980; SAZIMA 1980; GOULDING 1981; ARAGÃO 1981; CARVALHO 1981; FERREIRA 1981. 1984; SANTOS 1981, 1982; GOULDING & CARVALHO 1982; GOULDING & FERREIRA 1984; ALMEIDA et al. in press, and others).

These studies provide information about the frequency of different food items, assessed from stomach contents of the fish, but in only a few cases are they correlated with available food, or discussed in relation to interaction with other fish species in that habitat (LOWE-McCONNELL 1964; KNÖPPEL 1970; SOARES 1979; GOULDING 1981).

Within an ecosystem analysis frame work the fish fauna of Lago Camaleão, a floodplain lake on Marchantaria island near Manaus was studied in detail. In this paper, we will try to present a general account of the food availability in the lake and its utilization by the fish at medium and high waterlevels.

## 2. Description of the area

Lago Camaleão is a floodplain lake on Ilha de Marchantaria, the first island in the Amazon river above its confluence with the Rio Negro (Fig. 1). At mean waterlevel, the lake is up to 500 m broad, 7 km long and about 6 m deep. At high water, the whole island can be flooded, whereas at low water the lake is simply composed of some small pools, the largest of which is about 1 ha in area and about 1 m deep.

At low water, the dry lake bottom is covered with terrestrial and semi-aquatic grasses, sedges and herbaceous plants. With the onset of flooding many plants are inundated and killed, but others grow with the rising water and with free floating aquatic macrophytes, cover 50 - 75 % of the lake surface. The margins of the lake basin are covered by floodforest.

The water chemistry is strongly influenced by the Amazon river. However, during the low water period lake water is concentrated and there are strong biogenic modifications of its ionic composition (FURCH et al. 1983; FURCH 1984).

Because of the large amounts of decomposing organic material, oxygen concentration in the lake is very low and rarely exceeds 0.5 mg/l at the surface during the day. The water layer 2 m below the surface is oxygen free for many months. Improved aeration occurs during extremely high floods, when river water flows over the whole island, and at low water, when supersaturation with oxygen, due to high phytoplankton production and low water depth occurs in pools during the day (JUNK et al. 1983).

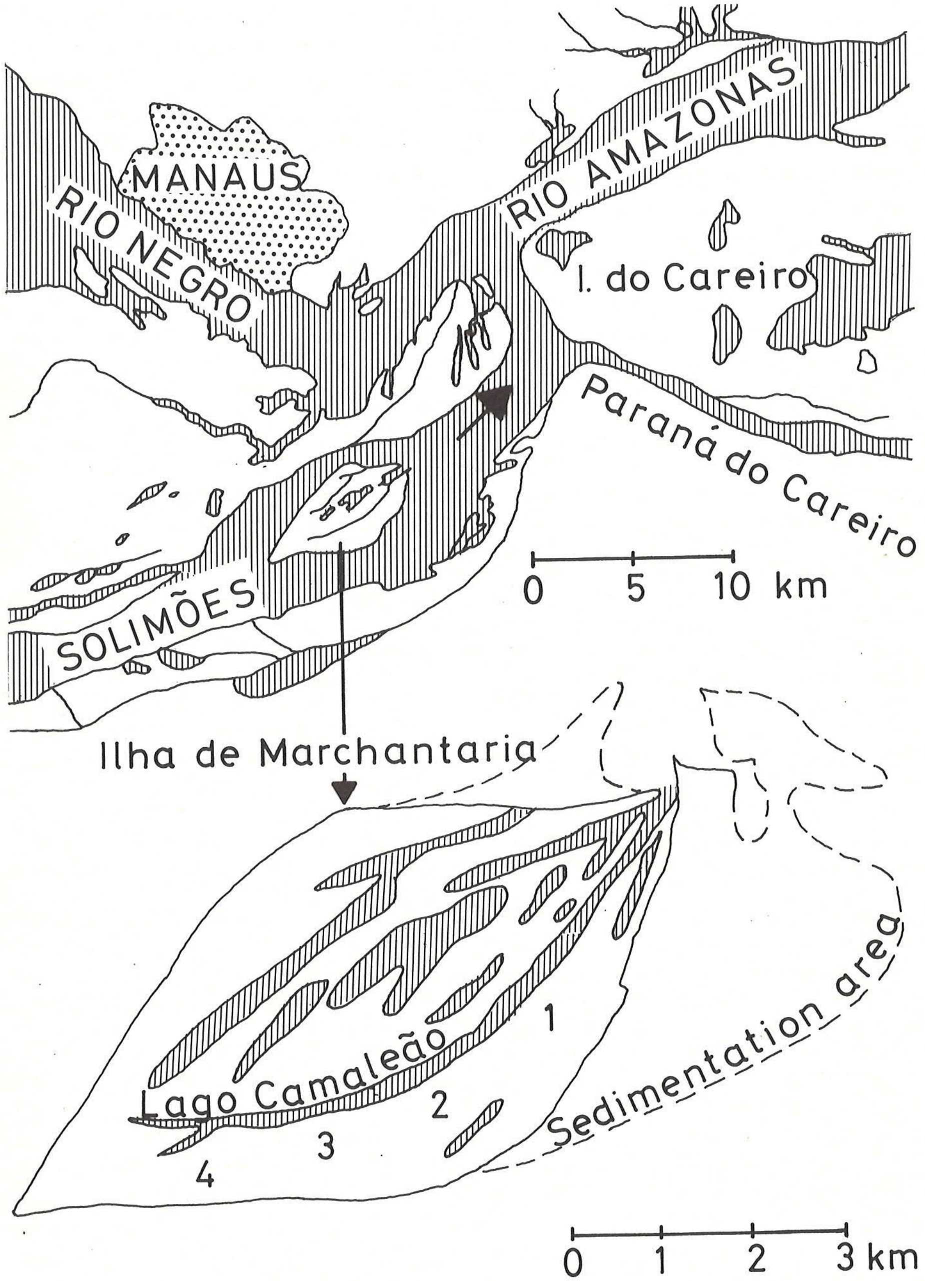

Fig. 1:
Map of the investigation area, indicating the 4 sampling stations.

The total number of fish species on the island is estimated to be about 200; 134 species have been recorded by JUNK et al. (1983) for the Lago Camaleão area and an oxygen rich bay in front of the lake. The fish fauna within the lake is rather species poor. About 40 species are able to colonize the lake permanently, under strongly hypoxic conditions. Most of them show morphological, anatomical and/or physiological adaptations to hypoxia. The majority of specimens caught in the lake were juveniles.

## 3. Materials and methods

In 1981 fish were caught at monthly intervals with seines (mesh size: 8 mm and 35 mm), and gillnets (mesh size: 6,9, and 12 cm) at 4 stations within the lake, in order to obtain a representative cross section throughout all habitats (JUNK et al. 1983). Sampling was not quantitative because of the abundant aquatic vegetation. However general information on the relative abundance of species was provided. Species were classified into 3 abundance classes: 1 = less than 1 %; 2 = 1 - 5 %; 3 = more than 5 % of total.

As the number of fish collected was very large, subsamples only were studied. Specimens were preserved in 10 % formalin, preservation being accelerated in large specimens by injection of formalin directly into the body. After 2 months the fish were transferred to 70 % ethanol solution. Taxonomy follows GÉRY (1977), KULLANDER (1983) and VARI (1984).

Stomach contents were identified under a binocular microscope. Proportions of different food items were estimated taking the total stomach content as 100 %, independent of its degree of fullness. The study period lasted from January to September, when the lake area was flooded and fish had abundant diverse food items at their disposal. During this period food uptake was rather uniform, showing no distinct pattern in most of the species. Therefore mean values are used to describe the trophic status. In October, at the beginning of the low water period, most fish left the area and only a few species remained in the permanent pools. Seasonality of food availability and uptake at high and low water will be dealt with in another paper.

Food items were categorized as follows:

**Aquatic macrophytes (AM):** fragments of leaves, stems, seeds and roots of aquatic and semiaquatic grasses, sedges and herbaceous plants, mostly *Paspalum* spp. *Oryza* spp. *Echinochloa polystachya, Salvinia* spp. *Lemna* spp.

**Material of the flooded forest (MF):** fragments of leaves, flowers, seeds and fruits of trees and bushes.

**Periphyton (PP):** sessile unicellular, colonial and filamentous algae.

**Detritus (D):** small and very small particles of dead organic material, often mixed with some periphyton and fungi.

**Zooplankton (Z):** Rotifera, Cladocera and Copepoda.

**Perizoon (PZ):** mostly larval stages of aquatic insects (Coleoptera, Diptera, Odonata, Hemiptera, Ephemeroptera) and some Mollusca.

**Terrestrial invertebrates (TI):** Hymenoptera (mostly Formicidae) Coleoptera, Orthoptera, Homoptera, Hemiptera, Dermaptera, Neuroptera, Isoptera, Diptera, Arachnida, Acari, Collembola.

**Fish (F):** all kind of fish and parts of fish (fins, scales).

## 4. Results

829 specimens, belonging to 34 species, 27 genera and 12 families were studied from January to September. These revealed the food and feeding habits of the Lago Camaleão fish fauna at medium and high waterlevel in 1981. 20 species consumed periphyton, 15 perizoon, 12 terrestrial invertebrates, 12 aquatic macrophytes, 11 fish, 10 detritus, 5 material from the flooded forest and 5 zooplankton. Quantities of each food category consumed varied (Table 1), but a considerable overlap in the utilization of the existing resources is shown, except for zooplankton and material from the flooded forest, which are each consumed by 5 species only.

Stomach contents of 16 species contained more than 75 % of a single food category, indicating a high degree of preference. 7 species fed predominantly on detritus, 6 on fish, 2 on material of the flooded forest and 1 on periphyton. The other 19 species had more than 25 % of at least two food categories in their stomachs (Table 2).

Comparison with data from other authors however shows that many species, depending upon their habitat, are able to consume a much wider variety of food items than is indicated by the stomach contents (KNÖPPEL 1970; SOARES 1979; GOULDING 1981; FERREIRA 1981, 1984; SANTOS 1981, 1982, and others). Taking this data into account 9 species are detritivorous and 4 are predatory (fish and decapod crustaceans). The adults of 2 species (*Colossoma macropomum, C. bidens*) feed mainly on fruits in the flooded forest. 13 species can be considered facultatively omnivorous, 4 are general herbivores and 4 are mixed predatory species, feeding on fish, terrestrial and aquatic invertebrates (mostly insects) (Table 3).

With regard to resource utilization in Lago Camaleão the abundance of different fish species has to be taken into consideration. Because of the lack of quantitative data available we used relative abundance data.

Table 1 shows that only 14 of the 34 species studied were abundant or very abundant in the lake (abundance classes 2 and 3). 12 species consume periphyton, 8 perizoon, 7 terrestrial invertebrates, 6 detritus, 5 aquatic macrophytes, 4 zooplankton, 3 material of the flooded forest and 1 fish. This indicates that the zooplankton, the material of the flooded forest and the fish are of little quantitative importance for the food webs in Lago Camaleão.

An attempt was made to quantify the importance of each food category for the entire fish fauna in Lago Camaleão. For this, the mean value of each food category (2.5 %, 15 %, 37.5 %, 62.5 %, 87.5 %) was multiplied by an abundance factor for each species according to the 3 abundance-classes indicated in table 1. Considering that these factors are arbitrary, three alternatives were calculated (Table 4). Because of the big size of *Osteoglossum bicirrhosum* and *Arapaima gigas* abundance class 2 was assumed for the calculation, despite its rare occurrence.

Results are given in figure 2. According to these calculations detritus is the most important food category, followed by terrestrial invertebrates, periphyton and aquatic macrophytes. The other food categories are of minor importance. Despite great differences in the abundance factors of the three calculated alternatives, the percentage of the different food categories is only little altered.

Table 1: Fish species of Lago Camaleão, their relative abundance and their main food categories as % of total stomach content (Average values from January to September 1981)

* 1 = < 1 %, 2 = 1 - 5 %, 3 = > 5 %

** I = 1 - 5 %, II = 5 - 25 %, III = 25 - 50 %, IV = 50 - 75 %, V = > 75 %

*** AM = Aquatic Macrophytes, MF = Material of the Flooded Forest, PP = Periphyton, D = Detritus, Z = Zooplankton, PZ = Perizoon, TI = Terrestrial Invertebrates, F = Fish, F* = Fish and Shrimps.

| Species | Abundance* | Nr. of stomachs | Food categories as % of stomach content**/*** | | | | | | | | Main food items cited by other authors |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AM | MF | PP | D | Z | PZ | TI | F | |
| FAM. OSTEOGLOSSIDAE | | | | | | | | | | | |
| *Osteoglossum bicirrhosum* | 1 | 8 | | | | | | | II | V | TI, MF |
| *Arapaima gigas* | 1 | 6 | | | | | | | | V | F |
| FAM. ERYTHRINIDAE | | | | | | | | | | | |
| *Hoplias malabaricus* | 1 | 10 | | | | | | | | V | F |
| *Hoplerythrinus unitaeniatus* | 1 | 5 | | | | | | | | V | PZ, TI |
| FAM. ANOSTOMIDAE | | | | | | | | | | | |
| *Schizodon fasciatus* | 1 | 22 | IV | | III | | | | | | AM, PP, MF |
| *Rhythiodus microlepis* | 1 | 21 | I | | V | | | | | | PP, MF |
| FAM. CURIMATIDAE | | | | | | | | | | | |
| SUBFAM. PROCHILODINAE | | | | | | | | | | | |
| *Prochilodus nigricans* | 1 | 33 | | | II | V | | | | | D |
| *Semaprochilodus taeniurus* | 3 | 40 | | | II | V | | | | | D |
| *S. insignis* | 3 | 40 | | | II | V | | | | | D |
| SUBFAM. CURIMATINAE | | | | | | | | | | | |
| *Potamorhina* cf. *altamazonica* | 2 | 42 | | | II | V | | | | | |
| *P. latior* | 3 | 39 | | | II | V | | | | | |
| *Psectrogaster curviventris* | 3 | 43 | | | II | V | | | | | |
| *Psectrogaster rutiloides* | 1 | 16 | | | II | V | | | | | |
| *Curimatella meyeri* | 1 | 22 | | | III | IV | | | | | |
| FAM. SERRASALMIDAE | | | | | | | | | | | |
| SUBFAM. SERRASALMINAE | | | | | | | | | | | |
| *Serrasalmus* sp. | 1 | 16 | | | | | | | | V | |
| *Mylossoma aureum* | 1 | 24 | IV | | II | | I | I | I | | |
| *M. duriventre* | 1 | 18 | IV | | II | | | II | | I | MF, AM |
| *Colossoma macropomum* | 2 | 49 | II | IV | | | | I | II | | MF, Z, PP |
| *C. bidens* | 1 | 20 | | V | | | | | | | MF |
| FAM. CHARACIDAE | | | | | | | | | | | |
| SUBFAM. BRYCONINAE | | | | | | | | | | | |
| *Brycon* cf. *melanopterus* | 1 | 22 | | V | | | | | II | | PP, TI, MF |
| *Triportheus angulatus* | 3 | 50 | III | I | I | | I | II | III | | AM, TI, MF |
| *T. albus* | 3 | 50 | III | I | II | | II | II | III | | AM, TI, Z |
| SUBFAM. TERAGONOPTERINAE | | | | | | | | | | | |
| *Ctenobrycon s. hauxwellianus* | 2 | 22 | III | | | III | III | | | | AM |
| *Odontostilbe fugitiva* | 3 | 39 | | | II | | | I | IV | | |

Table 1: Continuation.

| Species | Abundance* | Nr. of stomachs | Food categories as % of stomach content**/*** | | | | | | | | Main food items cited by other authors |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AM | MF | PP | D | Z | PZ | TI | F | |
| FAM. ELECTROPHORIDAE | | | | | | | | | | | |
| *Electrophorus electricus* | 1 | 2 | | | | | | | | V | F |
| FAM. CALLICHTHYIDAE | | | | | | | | | | | |
| *Hoplosternum thoracatum* | 2 | 24 | | | II | | II | III | III | | |
| FAM. LORICARIIDAE | | | | | | | | | | | |
| *Pterygoplichthys multiradiatus* | 2 | 21 | II | | II | IV | | II | | | |
| FAM. SYNBRANCHIDAE | | | | | | | | | | | |
| *Synbranchus marmoratus* | 1 | 21 | | | | | | IV | III | | F |
| FAM. CICHLIDAE | | | | | | | | | | | |
| *Astronotus ocellatus* | 1 | 22 | II | | | | | I | IV | II | MF, TI, PZ |
| *Cichlasoma amazonarum* | 1 | 15 | II | | | I | | IV | I | II | PP |
| *"Cichlasoma" temporale* | 1 | 12 | II | | | | | I | IV | | |
| *Heros severus* | 2 | 24 | | | IV | | | II | II | I | PP, MF |
| *Mesonauta festivus* | 2 | 29 | | | IV | | | II | | | PP, MF, AM |
| FAM. TETRAODONTIDAE | | | | | | | | | | | |
| *Colomesus asellus* | 1 | 2 | | | IV | | | II | | II | PZ, F* |
| Total | | 829 | | | | | | | | | |

Table 2: Utilization (as % of the stomach contents) of the different food categories by fish in Lago Camaleão (n = 34 species).

| Utilization % | I | II | III | IV | V | |
|---|---|---|---|---|---|---|
| Food category | 0 - 5 | 5 - 25 | 25 - 50 | 50 - 75 | > 75 % | n species |
| Aquatic Macrophytes | 1 | 5 | 3 | 3 | | 12 |
| Material of the Flooded Forest | 2 | | | 1 | 2 | 5 |
| Periphyton | 1 | 13 | 2 | 3 | 1 | 20 |
| Detritus | 1 | | | 2 | 7 | 10 |
| Zooplankton | 2 | 2 | 1 | | | 5 |
| Perizoon | 5 | 7 | 1 | 2 | | 15 |
| Terrestrial Invertebrates | 2 | 3 | 4 | 3 | | 12 |
| Fishes | 2 | 3 | | | 6 | 11 |

Table 3: Trophic characterization of the fish fauna of Lago Camaleão

**General herbivorous species:**
(Aquatic macrophytes, periphyton, leaves and fruits from the flooded forest)

| | |
|---|---|
| *Schizodon fasciatus* | FAM. ANOSTOMIDAE |
| *Rhythiodus microlepis* | FAM. ANOSTOMIDAE |
| *Mylossoma duriventre* | FAM. SERRASALMIDAE |
| *M. aureum* | FAM. SERRASALMIDAE |

**Fruit- and seed eating species:**
(Fruits and seeds from the flooded forest)

| | |
|---|---|
| *Colossoma macropomum* (adult) | FAM. SERRASALMIDAE |
| *C. bidens* (adult) | FAM. SERRASALMIDAE |

**Detritivorous species:**
(Fine or coarse detritus together with periphyton, fungi and bacteria)

| | |
|---|---|
| *Prochilodus nigricans* | FAM. CURIMATIDAE |
| *Semaprochilodus taeniurus* | FAM. CURIMATIDAE |
| *S. insignis* | FAM. CURIMATIDAE |
| *Potamorhina* cf. *altamazonica* | FAM. CURIMATIDAE |
| *P. latior* | FAM. CURIMATIDAE |
| *Psectrogaster curviventris* | FAM. CURIMATIDAE |
| *P. rutiloides* | FAM. CURIMATIDAE |
| *Curimatella meyeri* | FAM. CURIMATIDAE |
| *Pterygoplichthys multiradiatus* (? ) | FAM. LORICARIIDAE |

**Specialized predators:**
(Mainly fish, sometimes shrimps*)

| | |
|---|---|
| *Arapaima gigas* | FAM. OSTEOGLOSSIDAE |
| *Hoplias malabaricus* | FAM. ERYTHRINIDAE |
| *Serrasalmus* sp. | FAM. SERRASALMIDAE |
| *Electrophorus electricus** | FAM. ELECTROPHORIDAE |

**General predatory species:**
(Fish, shrimps, aquatic and terrestrial insects)

| | |
|---|---|
| *Osteoglossum bicirrhosum* | FAM. OSTEOGLOSSIDAE |
| *Hoplerythrinus unitaeniatus* | FAM. ERYTHRINIDAE |
| *Synbranchus marmoratus* | FAM. SYNBRANCHIDAE |
| *Astronotus ocellatus* (? ) | FAM. CICHLIDAE |

**Facultative omnivorous species:**
(Various types of plant-material and animals depending upon offer)

| | |
|---|---|
| *Colossoma macropomum* (juv.) | FAM. SERRASALMIDAE |
| *C. bidens* (juv.) | FAM. SERRASALMIDAE |
| *Brycon* cf. *melanopterus* | FAM. CHARACIDAE |
| *Triportheus angulatus* | FAM. CHARACIDAE |
| *T. albus* | FAM. CHARACIDAE |
| *Ctenobrycon* s. *hauxwellianus* | FAM. CHARACIDAE |
| *Odontostilbe fugitiva* (? ) | FAM. CHARACIDAE |
| *Hoplosternum thoracatum* (? ) | FAM. CHARACIDAE |
| *Cichlasoma amazonarum* | FAM. CICHLIDAE |
| *"Cichlasoma" temporale* | FAM. CICHLIDAE |
| *Heros severus* | FAM. CICHLIDAE |
| *Mesonauta festivus* (? ) | FAM. CICHLIDAE |
| *Colomesus asellus* (? ) | FAM. TETRAODONTIDAE |

Table 4: Theoretical % abundance of the three abundance classes using different abundance factors.

| | | | | |
|---|---|---|---|---|
| | Abundance class | 1 | 2 | 3 |
| | Abundance per definition | < 1 % | 1 - 5 % | > 5 % |
| I | Abundance factor | 1 | 10 | 100 |
| | Corresponding abundance | 0.11 % | 1.11 % | 11.12 % |
| II | Abundance factor | 1 | 5 | 25 |
| | Corresponding abundance | 0.39 % | 1.93 % | 9.65 % |
| III | Abundance factor | 1 | 4 | 10 |
| | Corresponding abundance | 0.76 % | 3.05 % | 7.63 % |

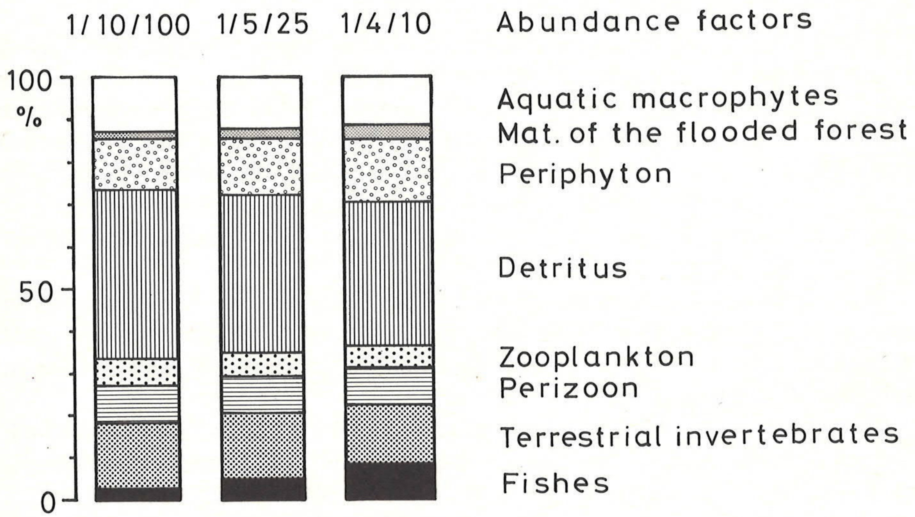

Fig. 2:
Importance of different food categories as % of the stomach content of 34 fish species of Lago Camaleão at different abundance factors for the abundance classes 1 = < 1 %, 2 = 1 - 5 %, 3 = > 5 %.

## 5. Discussion

### 5.1. The availability of food items

The most important sources of primary production in Lago Camaleão are terrestrial, aquatic and semi-aquatic grasses, sedges and herbaceous plants. JUNK (1985a) estimates net production during the dry period as 20 - 60 t dry weight/ha, depending upon species and the flooded biomass of dying vegetation at rising water as 10 - 40 t/ha. Similar values are reported from the flooded phase. Chemical analysis shows a protein content of 5 - 22 % and a relatively low cellwall content, giving the macrophytes rather high nutritional value (HOWARD-WILLIAMS & JUNK 1977). Seeds are of considerable importance and high nutrient value; in the case of wild rice they contribute up to 1 t/ha to the aquatic system.

An other important source of primary production is the flooded forest. ADIS & KLINGE (in press) record average litterfall as about 10 t dry weight/ha/a. According to BRAY & GORHAM (1964) the total production of tropical forests is 3.3 times greater than litterfall, giving a total annual production of about 33 t dry weight/ha/a. However, many leaves are of limited nutritional value for fish because of the high cell-wall content, low nutrient level and sometimes high polyphenol content (HOWARD-WILLIAMS 1974). Wood can be entirely excluded as a food item for fish. Flowers, fruits and seeds, amounting to about 1 t/ha/a dry weight are much more important.

Leaves of the flooded forest, in addition to roots and stems of the floating vegetation offer large surfaces for periphyton growth, despite shading by emergent parts of the macrophytes and trees. RAI & HILL (1984) estimate periphyton production of black-water lakes at 7.5 g $C/m^2/d$. The total periphyton production in Lago Camaleão is difficult to estimate because of the constantly changing surface area and light conditions in the lake due to water level fluctuations. It may be in the order of 5 - 10 t dry weight/ha/a. However, a considerable percentage of the periphyton is represented by Cyanophyceae which are of low food value for many fish.

Phytoplankton production in Lago Camaleão is low. Even considering a production capacity of 6 t/ha/a (SCHMIDT 1973), heavy surface shading by abundant floating macrophytes and the flooded forest, as well as competition for nutrients, reduce production to probably less than 1 t/ha/a.

The high amount of biomass, mainly produced by the terrestrial, semi-aquatic and aquatic macrophytes, results in considerable detritus production. Decomposition experiments in litterbags indicate high decomposition rates. HOWARD-WILLIAMS & JUNK (1976) recorded 50 % weight losses after 15 days. After 90 days 85 % of the initial weight were lost. However the results show that during the decomposition process a rather uniform detritus is produced, independent of the chemical composition of the initially exposed material, subsequently favouring detritivorous animals. Leaf weight loss is generally slower in the flooded forest, although there are considerable interspecific differences.

The large quantities of decomposing material produce strongly hypoxic conditions, which inhibit the occurrence of many aquatic invertebrates. Benthic animals are absent due to the $H_2S$ rich water layer near the ground. Investigation of the zooplankton reveals great species diversity for rotifers, but few, predominantly juvenile cladocerans and copepods, including species from the floating vegetation (KOSTE & ROBERTSON 1983; HARDY et al. 1984). In comparison with other floodplain lakes the zooplankton biomass is very small.

Low oxygen concentration and the occurrence of $H_2S$ reduces both abundance and species diversity of invertebrates colonizing the floating vegetation (JUNK 1973). Characteristic and abundant species e. g. *Cyclhestheria hislopi* (Conchostraca), *Macrobrachium* spp. and *Euryrhynchus* spp. (Decapoda) were completely absent in Lago Camaleão.

On the other hand, terrestrial invertebrates were abundant. Millions of ants, termites, spiders, caterpillars and collemboles are flooded out as the water rises. The floating vegetation is colonized by many specialized terrestrial invertebrates, which are caught by the fish, e. g. numerous semi-aquatic grasshoppers.

Numerous fish are themselves prey. BAYLEY (1982) estimates average annual fish biomass in the Amazon floodplain near Manaus as 160 $g/m^2 \pm 24$, with a mean annual production of 280 $g/m^2$. Furthermore, the Lago Camaleão fish are mostly juveniles and therefore of suitable size for consumption by predatory species.

### 5.2. Utilization of the food resources

The three calculated alternatives, despite strongly differing abundance factors, show only little shift in the percentage of food items in stomach contents, indicating that they provide a realistic picture of the trophic situation in Lago Camaleão (Fig. 2). Comparing the food availability with the stomach contents of the fish, we can state that while some resources are well represented others are not. Zooplankton and perizoon occur in small quantities in the lake and contribute correspondingly little as fish food. The flooded forest is also of low importance, mainly because of its marginal position around the lake. Terrestrial invertebrates and periphyton, which occur in great quantities in the lake are well represented in fish stomachs. Detritus is the major food item and can be considered as unlimited in the lake, at least during rising and high water periods. Fish and aquatic macrophytes as food items are markedly under-represented.

High predation pressure is generally characteristic for Amazonian inland waters. In the specific case of Lago Camaleão, the astonishingly low number of predators is considered a function of the extremely hypoxic conditions (JUNK et al. 1983) which only highly adapted species can tolerate. Obviously the great majority of predatory species are not able to colonize the lake most of the time. This hypothesis is supported by the high diversity and abundance of predators in the oxygen rich bay in front of the lake.

The small contribution of aquatic macrophytes to the stomach contents of the fish in a macrophyte dominated system is suprising and difficult to explain. Despite the enormous availability of a rather valuable food source, the lake has no fish species which feed specifically on macrophytes. 9 of the 12 species which do feed on them consume small quantities only (< 50 %). The three remaining species which have 50 - 75 % macrophytes in their stomachs, are considered in other habitats as general herbivores as they consume considerable amounts of periphyton and material from the flooded forest.

As already mentioned, due to the hypoxic conditions in the lake the fish fauna of Lago Camaleão is rather inpoverished and composed mainly of juveniles. However, even these conditions cannot satisfactorily explain the poor utilization of macrophytes. Several authors indicate that many members of the family Anostomidae and the subfamily Myleinae are macrophyte feeders (PAIXÃO 1980; GOULDING 1981; SANTOS 1981, 1982, and others).There are also some macrophyte feeders in the family Doradidae (e. g. *Lithodoras dorsalis*). However, all these species also feed to a considerable extent on other plant material e. g. fruits and seeds from the flooded forest, periphyton, filamentous algae etc.

The following hypothesis may explain the phenomenon. Firstly, present plant distribution is unnatural. Over the last centuries, man has considerably increased the area colonized by grasses, sedges and herbaceous plants as a result of large scale cutting and burning of the flooded forest for agriculture and the introduction of animal farming. At the same time he has greatly reduced the populations of large native herbivorous animals, the manatee (*Trichechus inunguis*), the capybara (*Hydrochoerus hydrochaeris*) and turtles (*Podocnemis* spp.). Thus, some centuries ago the availability of aquatic macrophytes was much less, whereas the demand by herbivorous animals was much greater.

Furthermore, aquatic macrophytes seem to be of limited food value for fish as a whole, as shown by the small number of specialized macrophyte feeders throughout the world. Other plant material, e. g. algae are of much higher nutritional value (about 40 % protein) than macrophytes. Fruits and seeds of the flooded forest are also superior to macrophytes as food.

The strong seasonality in the availability of aquatic macrophytes in Amazonia is an additional argument against them being a preferred food source. During periods of rising and high water level when macrophytes occur in great quantities, fish have many other and perhaps better food items at their disposal. According to JUNK (1976) and BAYLEY (1982), food is not a limiting factor for fish during that period. At low water level, when many food items become scarce, aquatic macrophytes are also scarce and may be absent during extreme drought. Some centuries ago this seasonality would have been even more pronounced, because macrophytes were less abundant, while macrophyte feeders such as manatees, capybaras and turtles were more frequent. Under these conditions omnivory or at least non-selective herbivory would be a better survival strategy than specialization on aquatic macrophytes.

Nutritional specialization by fish in the floodplains of Amazonian rivers is strongly influenced by the hydrological regime of the river and the related availability of food items. Constant availability of a food item seems to favour specialization. Detritivorous species, zooplankton feeders and unselective herbivorous species can find some food even at low water, although in reduced quantities. Predatory species may be even favoured during low water, when fish are crowded together in the remaining water bodies. Additional storage of fat during high water periods helps to overcome the critical period (JUNK 1985b).

Periodically available food items are exploited mainly by species with a rather broad food spectrum, or by a few highly adapted species, which deserve special mention. The juvenile tambaqui (*Colossoma macropomum*) is an omnivorous fish species which feeds on zooplankton, periphyton, aquatic macrophytes, fruits and seeds. The adult tambaqui feeds almost exclusively on fruits and seeds from the flooded forest, a periodically available food. According to GOULDING & CARVALHO (1982) this specialization is only possible because of the large body size of the fish and its capacity to accumulate huge amounts of fat during the high water period. This enables it to overcome the low water period without food. The manatee, a strictly aquatic herbivorous animal follows the same pattern. It also accumulates huge amounts of fat in its large body during high water and survives several months at low water without food.

The relatively low direct contribution of aquatic macrophytes to the stomach contents of fish in Lago Camaleão should not however lead to under-estimation of their role in the food web. A great part of the detritus, (at 30 - 40 % the main food item in Lago Camaleão) is probably derived from aquatic, semi-aquatic and terrestrial macrophytes. Periphyton, terrestrial invertebrates and perizoon, which contribute another 37 % of the food supply for fish, depend directly or indirectly upon the macrophyte stands, which provide a substratum, food and shelter.

On the other hand, negative impacts of the large macrophyte communities in Lago Camaleão to the trophic situation are obvious. Low contribution of strictly aquatic food items, e. g. zooplankton, benthos and some invertebrates from the perizoon to the fish diet is related to the macrophyte-induced strongly hypoxic conditions. Furthermore the macrophytes reduce phytoplankton abundance as a result of shading and competition for nutrients. Due to these multiple interactions the trophic situation in Lago Camaleão, and perhaps also in the entire floodplain of the Amazon river and its big whitewater tributaries, is much more complex than expected.

## 6. Summary

Food offer and consumption by the fish fauna were studied in Lago Camaleão, a macrophyte dominated and strongly hypoxic floodplain lake of the middle Amazon near Manaus. Of 34 investigated species, 16 can be considered specialized feeders on one type of food, whereas the others feed on two or more food types.

Major food items were detritus, periphyton and terrestrial invertebrates, which occur abundantly in the lake. Only small amounts of zooplankton and perizoon were consumed, but their biomass in the lake was also small due to the strongly hypoxic conditions. The flooded forest contributed only small amounts of food, because of its marginal position around the lake. In spite of their abundance fish and aquatic macrophytes were little consumed.

Whereas the absence of predatory species can be related to the strongly hypoxic conditions, the low aquatic macrophyte consumption is surprising. Low nutrient value compared to other abundantly available food items, and seasonality in macrophyte availability may be the reasons for the low direct consumption by the fish fauna.

## 7. Resumo

A oferta de itens alimentares e o seu consumo pelos peixes foram estudados no Lago Camaleão um lago de Várzea no médio Rio Amazonas perto de Manaus. O lago é dominado por macrófitas aquáticas e fortemente hipóxico.

Das 34 espécies ícticas estudadas, 16 podem ser consideradas como especializadas em um tipo de alimento, enquanto as outras consomen dois ou mais tipos de alimentos.

Os tipos de alimentos principais eram detritos, perifiton e invertebrados terrestres, os quais occorrem abundantemente no lago. Somente pequenas quantidades de zooplancton e perizoon foram consumidas, porém a sua biomassa no lago era pequena também por causa das condições fortemente hipóxicas. A floresta inundável contribuiu também somente com pouco alimento em virtude da sua posição marginal ao redor do lago. Peixes e macrófitas aquáticas foram pouco consumidos apesar de sua abundância no lago.

Enquanto a falta de espécies predadoras pode ser relacionada às condições fortemente hipóxicas, o baixo consumo de macrófitas aquáticas era surpreendente. O baixo valor nutritivo em comparação com outros ítens alimentares abundantes e uma sazonalidade na oferta de macrófitas aquáticas podem ser as razões para este fenômeno.

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